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An ecological study of sexual reproduction in *Trianthema portulacastrum* L. (Aizoaceae)

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ABSTRACT

Trianthema portulacastrum is an annual prostrate and ascending succulent herb. It produces distinct red and white flower morphs which grow in the same habitats but here white flower morph is quite common while the red flower morph is very rare. The flowers are bisexual, homogamous, self-compatible, open early morning and close back by noon. Spontaneous and vector-mediated pollination occurs; the vectors include thrips, bees and butterflies. Fruit set is almost 100% while seed set exceeds 80% in open pollinations indicating the function of facultative autogamy. Seed dispersal modes include autochory and hydrochory, the former enables continued invasion in parental sites while the latter enables invasion of new habitats. Seeds germinate immediately if the soil is not under water-stress and hence, the plant produces multiple generations, especially in wet season. Seeds are hard-seed coated, survive under the adverse conditions in the soil and germinate when favorable conditions return. The plant is widely used in traditional medicine and as a vegetable. Its exploitation for these uses is a potential remedy to control in areas where it is a menace. Its prolific growth in waste lands and open fields where vegetation is scarce is a natural control for soil erosion, a potential source of organic matter which improves water absorbing capacity of the soil.

Keywords: *Trianthema portulacastrum*, hermaphroditism, facultative autogamy, entomophily.

1. INTRODUCTION

Trianthema is a genus of Sesuvioideae sub-family in the family Aizoaceae. Around twenty species are known in this genus, eleven of them are endemic to northern and dry Australia (Prescott and Venning, 1984) and the rest in tropical and subtropical Asia and Africa (Bittrich and Hartmann, 1988; Wingfield and Newman, 1993). Many species of *Trianthema* occur in hottest places in the world such as Western Australian and Southwestern North American deserts (Correll and Johnston, 1996). The species are either annuals or perennials with prostrate growth form, fleshy leaves, bracteate inflorescences, flowers possessing five perianth segments subtended by a pair of bracts and circumscissile capsules with an aril completely sheathing the

seed (Bittrich and Hartmann, 1988; Wingfield and Newman, 1993). The taxonomic details of individual species, however, are not available.

Galinato et al., (1999) and Radanachaless and Maxwell, (1994) documented that *T. portulacastrum* is cosmopolitan with no known centre of origin and widespread in Southeast Asia, tropical America and Africa. In this species, two biotypes, red and green have been identified; both occur in India. Red biotype forms larger plants and reddish stems with long internodes and red flowers while green biotype is a smaller type and forms smaller plants which produce green stems with shorter internodes and flowers with green bracts, white perianth and green pods. The red biotype is more abundant, but the green one appears earlier in the season. In India, both red and green biotopes grow well under partial shade and thrive in neutral to alkaline soils with low organic matter. Rao and Reddy, (1982) reported that *T. portulacastrum* has two biotypes, red and green in India. The red biotype produces red flowers while the green one produces white flowers. Seeds from the red biotype are less dormant and germinate faster than those from the green biotype. Seeds germinate and produce flowers and seeds about one month after germination. Mohammed and Sen, (1990) reported that *T. portulacastrum* produces red and white flower morphs on different plants but they do not show any remarkable difference in their morphology, phenology and water relations. Metabolically, red flower morph is hardier than white flower morph because of lesser water loss, higher water retention capacity, high protein content and higher levels of proline accumulation at different stages of plant growth. Both flower morphs produce seeds with hard seed coat but seeds are hardier in white flower morph. These authors also documented that both red and white flower morphs show a wide distribution in arid zone but red morph is more aggressive and more drought-tolerant than the white flower morph.

Baylan and Bhan, (1986) reported that *T. portulacastrum* is a self-compatible species and able to proliferate under a range of warm temperatures. Dnyansagar and Malkhede, (1963) reported that *T. portulacastrum* possesses abundant viable 3-nucleate pollen grains at the time of shedding. Most of the pollen grains germinate soon and reach the embryo sac through the micropyle within 24 hours after pollination. Fertilization is porogamous. Bhargava, (1935) reported that fertilization in *T. monogyna* is also porogamous. Layek et al., (2015) reported that *T. portulacastrum* is pollinated by insect foragers such as *Apis cerana, A. florea, Trigona iridipennis*, *Augochloropsis metallica, Halictus* sp. (bees) and *Pseudoborbo bevani* (butterfly) which visit the flowers for nectar and pollen. This species is a major source of both nectar and pollen for *A. florea* colonies during dearth period in West Bengal, India. Dalio, (2015) reported that *T. portulacastrum* is a minor source of pollen and nectar for *Apis mellifera* during summer season in Punjab, India. However, this plant sustains *A. mellifera* colonies at critical time of floral scarcity. Sajjad et al., (2019) reported that *T. portulacastrum* is mostly visited by many individuals of *Pseudapis oxybeloides*. Kumar and Kumar, (2017) reported that *T. portulacastrum* is hermaphroditic and pollinated by insects. Its seeds are dispersed by water (hydrochory) and near the parent plant (autochory). Seeds may be dormant for few months. Wang et al., (2020) reported that *T. portulacastrum* with radial symmetry flowers without corolla tube is pollinated by butterflies and hawk moths. With this backdrop, the present study was conducted on the ecological aspects of sexual reproduction in *T. portulacastrum* and the outcome of the study is explained in the light of relevant literature.

2. MATERIALS AND METHODS

Trianthema portulacastrum L. populations growing in dry and wet areas near foothills of Visakhapatnam were selected for the study during wet season in 2019 and 2020. Phenological schedules, anthesis, anther dehiscence, floral morphology, flower closing behavior with reference to self-mediated autogamy, nectar and pollen characters, in vitro pollen germination, pollen-ovule ratio, stigma receptivity, flower visitors and their role in pollination, pollen carryover efficiency of insects to promote vector-mediated pollination rate, fruit and seed set rates in open-pollinations, fruit and seed characters and seed dispersal were examined very carefully according to the protocols provided in Dafni et al., (2005).

3. RESULTS

Phenology and floral morphology

It is an annual, prostrate to ascending succulent glabrescent herb which grows wild in open fields (Figure 1), waste lands and cultivated lands. It grows luxuriantly and displays flowering and fruiting simultaneously throughout the year at population level if water is available in the habitat. Its prostrate habit and profuse branching ability covers quickly the soil surface and forms a green carpet, especially in open fields. Individual plants are much-branched, glabrous, thickened and flattened at the nodes with a firm taproot system. Stem is slightly angular and glabrous with petiolate and ovate leaves which are dilated and sheathing at the base. Leaves are oppositely arranged pair-wise and connate into a funnel-shaped sheath. Profuse flowering occurs during July-September at population level. Flowers are solitary, sessile and born in leaf axils and the basal part especially ovary part of the flower is covered by sheathing stipule of bracts and connate bracteoles. They stand out prominently against the foliage. In the study area, the

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patches of this weed typically represent the white flower-morph. But, a few plants that represent red flower-morph occur with scattered distribution in the patches of white flower-morph.

Figure 1 *Trianthema portulacastrum* –Habit.

The flowers are small (6.6 ± 0.4 mm long and 8.1± 0.7 mm wide), white, odorless, actinomorphic and bisexual. The perianth has 5 white 5.1 ± 0.4 mm long and 2.8 ±0.3 mm wide petal-like tepals which are fused basally with the petiolar sheath. Stamens are commonly 15, free, 3-4 mm long and inserted near the basal fused part of the perianth; the filaments and anthers are white, glabrous and dorsifixed. The stamens number varies from 11 to 16 at population level; they are usually arranged in three whorls and each whorl is prominent by their height. The pistil is 6.3 ± 0.4 mm long consisting of superior green conical ovary with a single carpel and a single locule with 6-12 ovules (8.42 ± 1.32) arranged on basal placentation (Figure 2f, g), a single white linear papillose style and a simple wet and shiny, white papillose stigma. At population level, the ovule production rate per flower varies; 31% of flowers produce 8 ovules, 22% of flowers 9 ovules, 18% of flowers 10 ovules, 15% of flowers 7 ovules, 9% of flowers 6 ovules and 2% of flowers 2 ovules (Table 1).

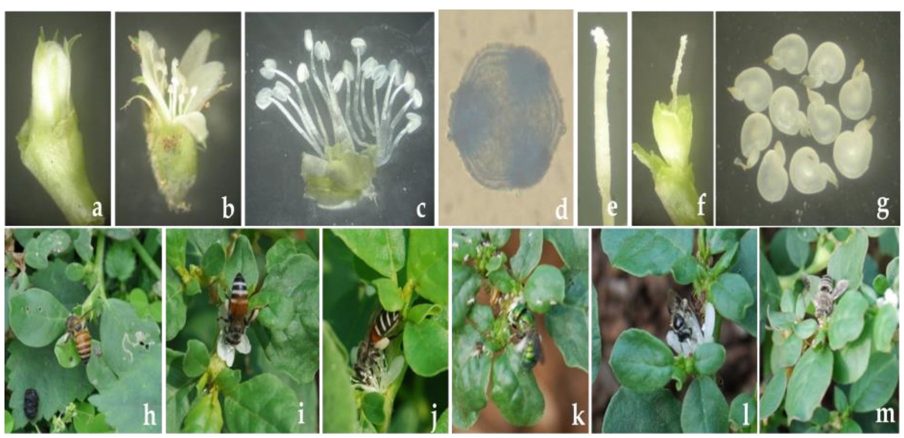

Figure 2 *Trianthema portulacastrum*: a. Mature bud, b. Flower, c. position of stamens and stigma, d. Pollen grain, e. Style and stigma coated with pollen, f. & g. Gynoecium with ten ovules, h. *Apis cerana*, i. & j. *Apis florea*, collecting nectar, k. *Ceratina smaragdula*, l. *Ceratina* sp., m. *Megachile* sp.

Table 1 Ovule production rate in *Trianthema portulacastrum*

No. of flowers sampled	Ovule production rate per flower											
	1	2	3	4	5	6	7	8	9	10	11	12
113	-	-	-	-	-	10	17	35	25	20	4	2
%	-	-	-	-	-	9	15	31	22	18	3	2
Range = 6-12; Mean ± S.D. = 8.42 ± 1.32												

Floral biology

Mature buds open during 0700-0800 h (Figure 2a, b) and anther dehiscence occurs simultaneously along with the opening of mature buds by longitudinal slits. The stamens spread out but stand erect after anthesis and the stigma is positioned centrally below the

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height of upper/middle whorl of stamens but above the lower whorl of stamens (Figure 2c). The pollen grains are white, dry, sub-prolate, tri-colporate, 20.9 ± 1.27 μm on polar axis, 16.8 ± 0.39 on equatorial axis, sparsely punctate (Figure 2d), 215.1 ± 26.76 per anther and 3,225 per flower; the pollen-ovule ratio is 384: 1. In vitro pollen viability test indicated that the pollen is viable with 72% viability at 0830 h and 9% at 1630 h (Table 2) indicating that it is viable for a few hours during day time on the day of anthesis. The stigma also attains receptivity during anthesis and continues until 1700 h of the day of anthesis. The nectar is produced in traces but it is mostly not available after anthesis due to nectar feeding activity by thrips during mature bud stage. The nectar has 6 essential amino acids which included threonine, valine, leucine, isoleucine, histidine and arginine and 9 non-essential amino acids which included alanine, amino-butyric acid, cysteine, cystine, glutamic acid, glycine, hydroxy- proline, proline and serine (Table 3). The tepals close back enclosing the pistil and stamens by 1200-1300 h on the day of anthesis; the stamens, style and stigma gradually wither and remain inside the persistent perianth which encloses the fruit for protection.

Table 2 In vitro pollen germination in *Trianthema portulacastrum*

Pollen storage time (h)	No. of pollen grains	No. of pollen grains geminated	Germination (%)
0830	100	72	72
0930	100	71	71
1030	100	65	65
1130	100	52	52
1230	100	36	36
1330	100	30	30
1430	100	24	24
1530	100	12	12
1630	100	9	9
1730	100	0	0

Table 3 Essential and non-essential amino acids present in the nectar of *Trianthema portulacastrum*

Essential amino acids		Non-essential amino acids	
Amino acid type	Present (+)/ Absent (-)	Amino acid type	Present (+)/ Absent (-)
Threonine	+	Alanine	+
Valine	+	Amino butyric acid	+
Methionine	-	Aspartic acid	-
Leucine	+	Cysteine	+
Iso leucine	+	Cystine	+
Lysine	-	Glutamic acid	+
Phenyl alanine	-	Glycine	+
Histidine	+	Hydroxy proline	+
Arginine	+	Proline	+
Tryptophan	-	Serine	+
		Tyrosine	-

Flower behavior and pollination

In mature buds which are about to open the perianth, the stamens are in erect state but the centrally seated linear style and stigma is positioned below the height of upper/middle whorl of stamens and above the height of lower whorl of stamens. With simultaneous function of male and female sex by the dehiscence of anthers and attainment of stigma receptivity during anthesis, the flowers facilitate the occurrence of spontaneous autogamy (Figure 2e) with the pollen of upper/middle whorl of stamens but not with lower whorl of stamens. After anthesis, the tepals gradually expand and become nearly flat during which the linear style and stigma stands erect and the stamens spread apart to prevent the occurrence of spontaneous autogamy and provide opportunity for the occurrence of vector-mediated geitonogamy and xenogamy during the open state of the flowers. By noon or slightly after noon, the perianth closes back bringing back the upper and middle whorl of stamens close to the stigma; this positional shift of stamens and

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their placement above the stigma facilitate again the occurrence of self-pollination by the gravitational fall of dry pollen on the downwardly placed stigma which is still in receptive state. The occurrence of self-pollination at flower closure time depends on the availability levels of pollen in the anthers. Further, the closed flowers do not deter the thrips from entering into the flower and their intra-floral movements for forage collection even during the closed state of the flowers result in self- and/or cross-pollination as the stigma is receptive until the evening of the day of anthesis. Therefore, the flower behavior involving movements of tepals and stamens provide ample opportunities for the occurrence of spontaneous or vector-mediated self- and/or cross-pollination.

Insect visitors and pollination

Thrips-pollination

The buds were used by terebrantian thrips, *Megalurothrips distalis* Karny and *Frankliniella schultzei* Trybom (Family: Thripidae, Sub-family: Thripinae) for their breeding. They moved out during anthesis process with the unfolding of the perianth to expose the sex organs. These thrips remained on the plant as resident foragers and foraged for both pollen and nectar which are available or accessible during and after anthesis and also after flower closure. Bud infestation with thrips was 79%. The forage collection and crawling of the thrips within and between flowers on the same plant were considered to be effecting autogamy and geitonogamy. The thrips also moved to adjacent plants by crawling because of the growth of the plant populations as extensive mats and also by flying in order to collect pollen and nectar from different plants and this forage collection behavior was considered to be effecting cross-pollination also. The papillose stigma captures the pollen with great ease from the pollen-laden thrips when the latter crawl on the stigma which ensures the occurrence of pollination.

Bee and butterfly-pollination

The flowers were foraged regularly by bees and butterflies during day-time, the former for pollen and nectar while the latter for nectar only (Table 4). The foraging activity of these insects was very high at profuse flowering phase which occurs during rainy season. Both bees and butterflies foraged during 0800-1100 h with maximum activity at 0900 h (Figure 4). The bees collected both pollen and nectar mostly in the same visit to the flowers. The bees were *Apis cerana* (Figure 2h), *A. florea* (Figure 2i, j), *Trigona iridipennis*, *Ceratina smaragdula* (Figure 2k), *Ceratina* sp. (Figure 2l) and Megachile sp. (Figure 2m). The butterflies represented lycaenids only which included *Castalius rosimon*, *Zizeeria karsandra* (Figure 3a), *Zizina otis* (Figure 3b), *Chilades laius* (Figure 3c) and *Euchrysops cnejus* (Figure 3d). Of the total foraging visits made by insects, bees made 66% and lycaenid butterflies 34% (Figure 5). The flowers with actinomorphic symmery and completely exposed sex organs facilitated landing and probing for both pollen and/or nectar with great ease by bees as well as butterflies; while collecting forage, these insects effected pollination. The pollen carrying capacity evaluated by body washings (except corbiculae on hind legs in case of bees) of insects captured at 0900-1000 h indicated that the bees were more efficient in carrying pollen than butterflies. *A. cerana* carried 59.7 ± 18.69, *A. florea* 45.8 ± 15.76, *T. iridipennis* 31.9 ± 9.12, *Ceratina smaragdula* 26.8 ± 9.55, *Ceratina* sp. 35.1 ± 11.55 and *Megachile* sp. 34.3 ± 11.98 pollen grains. The average number of pollen grains recovered in the washings of head, proboscis and body of lycaenid butterflies varied from 16.6 ± 4.29 to 13.3 ± 3.74 (Table 5).

The forage collection activity by all insect species was found to be resulting in self- and/or cross-pollination depending on the pollen source from the same or different conspecific individual plants which are closely spaced carpeting the soil. The foraging activity of thrips for nectar as well as pollen was found to be driving the bees to make multiple visits to the same and/or different flowers on the same or different conspecific plants in the habitat collect forage to the extent possible well in advance to the flower closure. Thrips bring about self-pollination mostly during and after anthesis and in closed flowers as well while bees and butterflies bring about both self- and/or cross-pollination during the open state of the flowers. Therefore, insect foraging activity was considered to be important in achieving cross-pollination which ensures the occurrence of genetic variation.

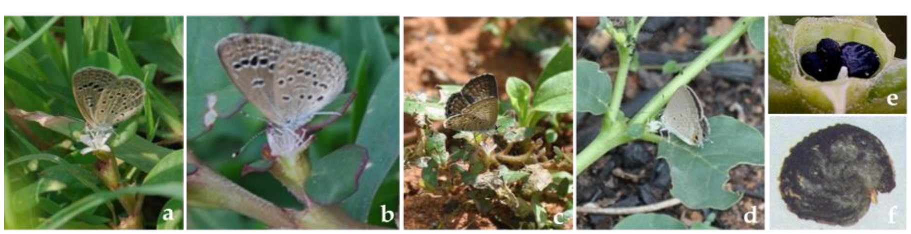

Figure 3 *Trianthema portulacastrum:* a-d*: Lycaenid butterflies -* a. *Zizeeria karsandra,* b. *Zizina otis,* c. *Chilades laius,* d. *Euchrysops cnejus,* e. & f. Seeds.

Table 4 List of insect foragers on *Trianthema portulacastrum*

Order/Family	Insect species	Common name	Forage sought
Hymenoptera			
Apidae	*Apis cerana* F.	Indian Honey Bee	Pollen + Nectar
	Apis florea F.	Dwarf Honey Bee	Pollen + Nectar
	Trigona iridipennis Smith	Stingless Bee	Pollen + Nectar
	Ceratina smaragdula F.	Small Carpenter Bee	Pollen + Nectar
	Ceratina sp.	Small Carpenter Bee	Pollen + Nectar
Megachilidae	*Megachile* sp.	Leafcutter bee	Pollen + Nectar
Lepidoptera			
Lycaenidae	*Castalius rosimon* F.	Common Pierrot	Nectar
	Zizeeria karsandra Moore	Dark Grass Blue	Nectar
	Zizina otis F.	Lesser Grass Blue	Nectar
	Chilades laius Stoll	Lime Blue	Nectar
	Euchrysops cnejus F.	Gram Blue	Nectar

Table 5 Pollen recorded in the body washings of bees and butterflies foraging on *Trianthema portulacastrum*

Insect species	Sample size (N)	Number of pollen grains recorded		
		Range	Mean	S.D
Apis cerana	10	28-93	59.7	18.69
Apis florea	10	24-81	45.8	15.76
Trigona iridipennis	10	19-52	31.9	9.12
Ceratina smaragdula	10	17-48	26.8	9.55
Ceratina sp.	10	18-57	35.1	11.55
Megachile sp.	10	20-62	34.3	11.98
Castalius rosimon	10	9-23	13.3	3.74
Zizeeria karsandra	10	8-25	16.4	6.10
Zizina otis	10	7-22	14.6	4.69
Chilades Laius	10	10-25	16.6	4.29
Euchrysops cnejus	10	9-27	13.7	3.27

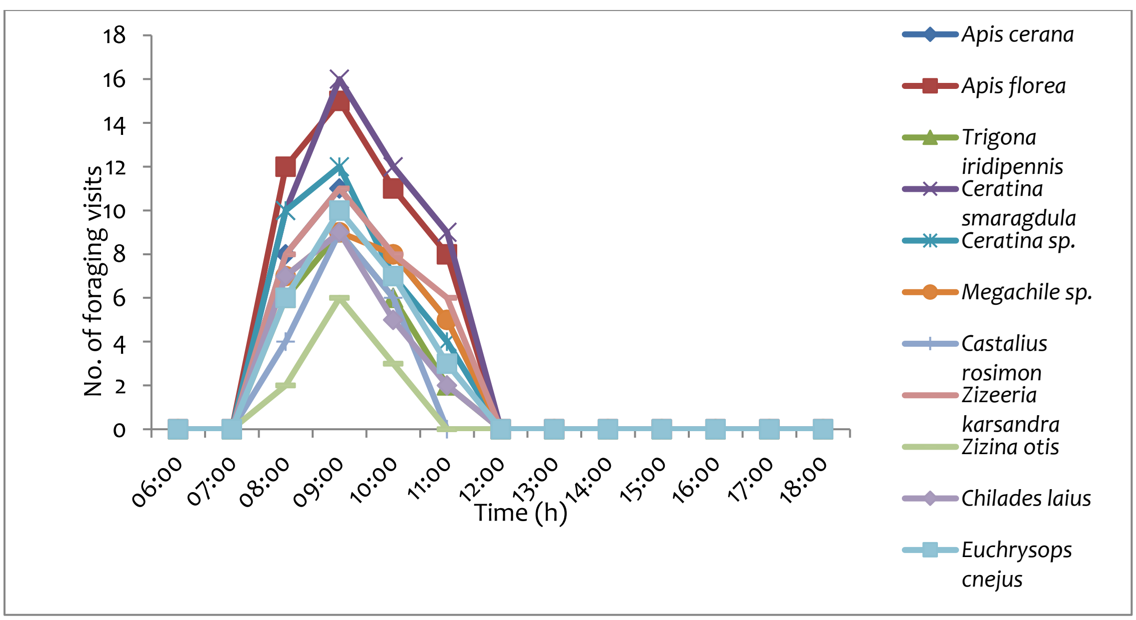

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Figure 4 Hourly foraging activity of bees and butterflies on *Trianthema portulacastrum*

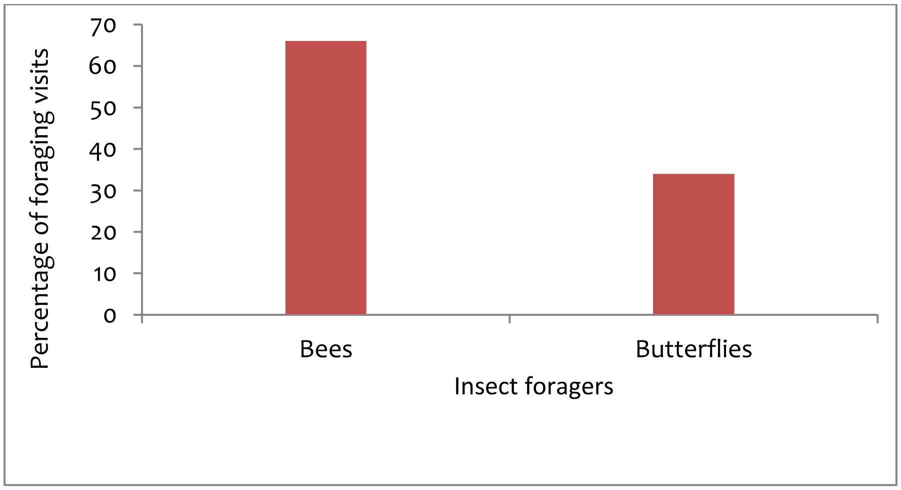

Figure 5 Percentage of foraging visits of bees and butterflies on *Trianthema portulacastrum*

Table 6 Seed production rate in *Trianthema portulacastrum*

No. of fruits sampled	Seed production rate per fruit											
	1	2	3	4	5	6	7	8	9	10	11	12
114	-	-	-	7	22	18	30	21	9	5	2	0
%	-	-	-	6	19	16	26	18	9	4	2	
Range = 4-11; Mean ± S.D. = 6.84 ± 1.6												

Fruiting ecology

Fruit initiation and maturation takes place within two weeks after pollination and fertilization. Fruit set rate is 98% while seed set rate is 81% in open-pollinations. Seed production rate per fruit varies at population level; 26% of fruits produced 7 seeds, 19% of fruits 5 seeds, 18% of fruits 8 seeds, 16% of fruits 6 seeds, 9% of fruits 9 seeds, 6% of fruits 7 seeds, 4% of fruits 10 seeds and 2% of fruits 2 seeds (Table 6). Seed production rate per fruit is 6.84 ± 1.6. Fruit is a circumscissile capsule with corky pericarp with a winged lid, 4.7 ± 0.7 mm long, 3. 23 ± 0.2 mm wide and basally enclosed by the perianth and partly concealed in the petiolar hood. Fruit dehiscence is characterized by the winged lid breaking off from the basal part due to horizontal line that runs all the way around the fruit to separate the lid. The lid part of the fruit carries away 1 or 2 seeds upon capsule dehiscence while the remaining seeds are still intact with the basal portion of the fruit. The seeds that remained in the dehisced fruit fall out after the plant dies and withers. The seeds dispersed by detached winged lid and those subsequently fall to the ground from the basal portion of the fruit settle in the vicinity of the parental sites and carried away by rain water during wet season. Seeds are black, reniform, not shiny, hard seed coated, 1.5-2.3 mm long with faint wavy ribs and a small strophiole (Figure 3e, f). Seeds dispersed during rainy season germinate immediately while those dispersed from the plants at other times germinate depending on the moisture content of the soil. The germinated seeds produce flowers and seeds within five weeks. The plant has the ability to produce multiple generations if the habitat is sufficiently wet and nutrient-rich.

4. DISCUSSION

Trianthema species are either annuals or perennials with prostrate growth form, fleshy leaves, bracteate inflorescences, flowers possessing five perianth segments subtended by a pair of bracts and circumscissile capsules with an aril completely sheathing the seed (Bittrich and Hartmann, 1988; Wingfield and Newman, 1993). The present study shows that *T. portulacastrum* is an annual prostrate and ascending succulent glabrescent herb with solitary flowers possessing five perianth segments subtended by a pair of bracts and producing circumscissile capsule with seeds lacking a typical aril but it is substituted by a small strophiole.

Mohammed and Sen, (1990) reported that *T. portulacastrum* produces red and white biotypes, both types show a wide distribution in arid zone in Rajasthan but the red type is more aggressive and is more drought tolerant than the white type. Red biotype produces red or light pink flowers while white biotype produces white flowers; both types produce 10 to 25 short and long-stalked stamens with the latter being in higher frequency. In the study area, both red and white flower forms representing two

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different biotypes reported by Mohammed and Sen, (1990) occur intermingled with each other in the same habitats but the plants producing red flower morph are rare while those producing white flower morphs are quite common. The habitats of the study area represent semi-dry to wet soil environment which is conducive for the luxuriant growth of white biotype and the red biotype appears to have evolved to tolerate drought conditions and grow luxuriantly in arid zones. In the study area, *T. portulacastrum* carpets the soil in open fields and waste lands and produces multiple generations depending on the status of soil moisture but prolific growth, flowering and fruiting occur during rainy season only.

Layek et al., (2015) reported that *T. portulacastrum* flowers open early morning at 0630-0700 h with anther dehiscence occurring 30 minutes after anthesis. In this study, *T. portulacastrum* shows anthesis during 0700-0800 h with simultaneous occurrence of anther dehiscence and attainment of stigma receptivity; the function of homogamy and the closely spaced upper and middle whorl of stamens above the linear stigma enable the occurrence of spontaneous autogamy during anthesis and again during flower closure which takes place at noontime. Further, thrips also effect self- and/or cross-pollination by their feeding on pollen and nectar during and after anthesis and during and after flower closure. But, spontaneous autogamy or thrips-mediated pollination after flower closure occurs until the stigma becomes unreceptive to pollen by which time the pollen also becomes inviable. This study agrees with Dnyansagar and Malkhede, (1963) who reported that in *T. portulacastrum* most of the pollen grains germinate soon and reach the embryo sac through the micropyle within 24 hours after pollination.

Milton et al., (1997) considered that Aizoaceae species are self-incompatible. Baylan and Bhan, (1986) reported that *T. portulacastrum* is a self-compatible species. In this study, *T. portulacastrum* produces almost cent percent fruit set and more than 80% seed set in open-pollinations indicating that it is self-compatible, primarily self-pollinating and hence, facultative autogamy is functional which is further substantiated by the brief duration of open state of flowers. The variation in ovule number per flower is in a way a mechanism evolved by the plant to economically utilize the nutrient resources available to the plant and at the same time maximize seed set rate. Cruden, (1977) reported that pollen-ovule ratios can serve as a reliable indicator of breeding system. High pollen-ovule ratio is normally associated with obligate out-crossing, moderate pollen-ovule ratios with facultative xenogamy and low pollen-ovule ratios with obligate autogamy. In this study, it is found that *T. portulacastrum* produces moderate pollen-ovule ratio according to Cruden, (1977), which is an indication of facultative xenogamy. But, facultative autogamy is functional in *T. portulacastrum* and the excess pollen production at flower level appears to compensate the pollen loss due to hectic pollen collection activity by bees and make available enough pollen for vector-mediated pollination to achieve cross-pollination and the associated genetic variation.

Different authors reported that *T. portulacastrum* is either a major or minor source of pollen and nectar in different areas. Layek et al., (2015) reported that *T. portulacastrum* is a major source of nectar and pollen for *A. florea* colonies during dearth period in West Bengal, India. Dalio, (2015) reported that *T. portulacastrum* is a minor source of pollen and nectar for *Apis mellifera* and sustains *A. mellifera* colonies at critical time of floral scarcity during summer season in Punjab, India. Sajjad et al., (2019) reported that *T. portulacastrum* is mostly visited by many individuals of *Pseudapis oxybeloides* which is a voracious pollen gatherer in Pakistan. These reports indicate that *T. portulacastrum* is under tremendous stress to overcome the pollen loss from voracious pollen gathering activity of bees and as a result this plant might have resorted to gradually increase pollen production rate at flower level and hence at population level to attract bee pollinators and use them to achieve cross-pollination, in particular in order to maintain genetic variation which is essential to survive as a successful weed.

Chesselet et al., (2001) reported that many species of Aizoaceae produce abundant pollen as an important reward to attract insects and achieve pollination. Bittrich, (1987) suggested that the abundant pollen might be an adaptation for wind pollination. Ihlenfeldt, (1994) noted that many species of Aizoaceae attract a wide spectrum of floral visitors. Struck, (1994) noted that most of the Aizoaceae species display entomophilous pollination syndromes. Leyek et al., (2015) reported that *T. portulacastrum*, a member of Aizoaceae family is pollinated by bees such as *Apis cerana, A. florea, Trigona iridipennis*, *Augochloropsis metallica* and *Halictus* sp., and the hesperiid butterfly, *Pseudoborbo bevani* in West Bengal, India. Wang et al., (2020) reported that *T. portulacastrum* is pollinated by butterflies and hawk moths in Xisha Islands in China. In this study, *T. portulacastrum* has been observed to be pollinated by insects consisting of bees and lycaenid butterflies and thrips as resident foragers. The nectar is a source of some essential and non-essential aminoacids for the flower visitors. The foraging activity by bees and butterflies is very brief because the flowers close back within six hours and the possibility for insect-mediated pollination, especially cross-pollination is regulated as the plant displays facultative autogamy mating system. However, thrips foraging activity by reducing the availability of standing crop of nectar and pollen indirectly drive bees and butterflies to increase their foraging visits to collect forage during the brief period of open state of flowers, due to which pollination rate is maximized.

Parolin, (2006) reviewed seed dispersal syndromes in Aizoaceae. He reported that ninety eight percent of the species possess hygrochastic capsules with an ombrohydrochoric seed dispersal mechanism. Kumar and Kumar, (2017) reported that *T.*

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portulacastrum is hydrochorous and autochorous. In this study, it is found that *T. portulacastrum* fruits dehisce by circumscissile fashion to fly off the winged lid to disperse seeds. The winged lid carries 1 or 2 seeds which fall to the ground subsequently in the parental site; this mode of dispersal characterizes autochory. After fruit dehiscence, the basal half of the fruit contains several seeds which are dispersed only when the plant dies and withers, in this case also, the seeds fall in the parental site. Subsequently, the seeds dispersed by winged lid and those dispersed following the death of the plant will be dispersed by rain water from parent sites to other sites during wet season; this mode of seed dispersal is the characteristic of hydrochory and this mode is very important for the plant to arrive at new sites or habitats and expand its distribution range.

Seed germination ecology

Baylan and Malik, (1989) reported that *T. portulacastrum* has enormous seedling capacity or very little dormancy that allows the mature seed to germinate immediately to produce multiple generations in the same season. Kaur and Aggarwal, (2017) reported that in *T. portulacastrum*, enormous seed production and low dormancy leads to a large seed bank in the soil and enables the plant to survive in the adverse condition. Kumar and Kumar, (2017) reported that *T. portulacastrum* seeds may be dormant for a few months. Tanveer et al., (2013) reported that *T. portulacastrum* has potential to germinate or emerge under varying ecological conditions. In this study, it is observed that *T. portulacastrum* is a copious seed producer and the seeds germinate immediately if the soil is not under water-stress. With this ability, the plant produces multiple generations in the same season, especially in wet season. Seeds being hard-seed coated have the ability to survive under the adverse conditions in the soil and germinate when favorable conditions return. The seeds upon germination produce new plants and flowers and seeds after one month (Verma, 2013).

Physiological adaptations (based on documented information)

Baylan and Bhan, (1986) reported that *T. portulacastrum* is able to proliferate under a range of warm temperatures. Branch, (2016) reported that *T. portulacastrum* is a heat-adapted species because it has evolved impressive reproductive thermal tolerance to withstand extreme heat stress. Berry and Bjorkman, (1980) and Prasad et al., (2006) reported that *T. portulacastrum* is a C_4 herb and has a greater capacity to photosynthesize at high temperatures in comparison to C_3 species. Lundgren et al., (2015) reported that C_4 species are usually abundant in warm but not cool environments and this photosynthetic pathway is physiologically advantageous for their niche broadening in warm environments. Williams et al., (2013) stated that C_4 plants grow faster than C_3 plants, require less water; C_4 photosynthesis prevents wastage of a lot of energy and resources. As *T. portulacastrum* has different abilities such as tolerance to extreme heat stress, carry out photosynthesis and niche broadening in warm environments by saving a lot energy and water resource, it is a promising species to exploit its genetic pool to develop heat-adapted crop plants in the context of rising global temperatures and the looming possibility of widespread crop failure (Branch, 2016).

Medicinal, vegetable and ecological values (based on documented information)

Bhattacharya and Chatterjee, (1998) and Aguilar, (2001) documented that *T. portulacastrum* has a long history of folklore medicine in India, Bangladesh, The Philippines and other Asian countries. In India, the plant is used as a vegetable and considered to be efficacious in the treatment of several diseases. In view of the importance of *T. portulacastrum* in traditional medicine and as a vegetable, its exploitation for these uses is a potential remedy to control its menace especially in agricultural fields. Its prolific growth in waste lands and open fields where vegetation is scarce is a natural control for soil erosion and a potential source of organic matter to add soil fertility (Kirtikar and Basu, 2003; Ambasta, 1986; Gaddeyya et al., 2017) and improve infiltration and percolation rates of water into the ground. Therefore, *T. portulacastrum* can be used as a potential candidate in the ecological restoration of degraded and damaged habitats.

5. CONCLUSIONS

Trianthema portulacastrum is an annual prostrate and ascending succulent ruderal and agrestal herbaceous weed. In this species, red and white biotype, the former producing red flowers and the latter producing white flowers occur intermingled with each other in the same habitats but the plants producing red flower morph are rare while those producing white flower morphs are quite common. Spontaneous autogamy occurs during anthesis and flower closure period. Bees and lycaenid butterflies and also thrips act as pollinators. Fruit set is almost cent percent while seed set rate exceeds 80% in open-pollinations indicating that it is self-compatible, primarily self-pollinating and hence, facultative autogamy is functional which is further substantiated by the brief duration of open state of flowers. The fruit is a circumscissile capsule. Seed dispersal modes include autochory and hydrochory. The plant is widely used in traditional medicine and as a vegetable. Its exploitation for these uses is a potential remedy to control its

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menace especially in agricultural fields. Its prolific growth in waste lands and open fields where vegetation is scarce is a natural control for soil erosion, a potential source of organic matter to add soil fertility and improve infiltration and percolation rates of water into the ground. This plant with C4 mechanism has different abilities such as tolerance to extreme heat stress, carrying out photosynthesis efficiently, broadening niches in warm environments by saving a lot energy and water resource. These abilities indicate that these plant species are promising species to exploit their genetic pool to develop heat-tolerant crop plants in the context of rising global temperatures and the looming possibility of widespread crop failure.

Authors contributions

All work contributed by this author only.

Ethical approval

Trianthema portulacastrum L. species from foothills of Visakhapatnam was used in the study. The ethical guidelines for plants & plant materials are followed in the study for sample collection & identification.

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Conflicts of interests

The authors declare that there are no conflicts of interests.

Data and materials availability

All data associated with this study are present in the paper.

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